The inheritance of resistance to Rhynchosporium secalis in Ethiopian barley cultivars
by Segenet Kelemu

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Plant Pathology
Montana State University

Abstract:
Barley scald is one of the most economically important diseases prevailing in cool, humid areas of the world. The disease can effectively be controlled by the use of resistant cultivars. This investigation was initiated to determine the number of gene loci conditioning resistance to barley scald in newly identified resistant Ethiopian barley cultivars and relate their genes to some of those previously reported. Fi, BC1, F2 and F3 progeny from different cross combinations were tested with seven isolates of Rhynchosporium secalis under controlled environment conditions. Adult F2 plants were also evaluated for their reaction to an isolate from Montana under field conditions.

. Five resistance genes, which were shown to be different from the previously reported genes, were identified in four Ethiopian cultivars. Three of these genes were dominant in action and two recessive. The symbols Rhl2 and Rh 13 were proposed for the dominant genes identified in PI-382282 and PI-382509, rhl4 for the recessive gene in PI-382282 and rhl5 and Rhl6 for the recessive and dominant genes found in PI-383036 and PI-382471, respectively. One Ethiopian barley, PI-383036, was shown to possess a gene at the Rh-Rh3-Rh4 complex locus.

Indication was found for the existence of cytoplasmic effects on scald resistance in some cross combinations.

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This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citation, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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E. L. Sharp — Chairperson, Graduate Committee

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ABSTRACT

Barley scald is one of the most economically important diseases prevailing in cool, humid areas of the world. The disease can effectively be controlled by the use of resistant cultivars. This investigation was initiated to determine the number of gene loci conditioning resistance to barley scald in newly identified resistant Ethiopian barley cultivars and relate their genes to some of those previously reported. F_1, BC_1, F_2 and F_3 progeny from different cross combinations were tested with seven isolates of *Rhynchosporium secalis* under controlled environment conditions. Adult F_2 plants were also evaluated for their reaction to an isolate from Montana under field conditions.

Five resistance genes, which were shown to be different from the previously reported genes, were identified in four Ethiopian cultivars. Three of these genes were dominant in action and two recessive. The symbols Rh12 and Rh13 were proposed for the dominant genes identified in PI-382282 and PI-382509, rh14 for the recessive gene in PI-382282 and rh15 and Rh16 for the recessive and dominant genes found in PI-383036 and PI-382471, respectively. One Ethiopian barley, PI-383036, was shown to possess a gene at the Rh-Rh3-Rh4 complex locus.

Indication was found for the existence of cytoplasmic effects on scald resistance in some cross combinations.

CHAPTER 1

INTRODUCTION

Barley is one of the most important cereal crops contributing immeasurably to the world's food and feed production.

Barley serves as an experimental plant for numerous studies. It is among the top half-dozen plant species in the number of gene loci plotted on linkage maps, probably because of its small number of chromosomes and the large number of clearly classifiable characters.

The many varietal types of barley have a wide ecological range and diverse adaptabilities which can be seen from the fact that cultivation is widespread from north to south and from lowland areas below sea level to high mountain ranges. Barley grows beside frozen pools in highland Ethiopia, and beneath date palms in the Sahara desert (Weaver, 1950). It is considered to be man's most dependable grain crop because of its ability to mature earlier than any other cereal and, as a result, escape drought or cold (Nuttonson, 1957).

There are two main centers of diversity of barley according to Vavilov. One, pivoting around Abyssinia (Ethiopia) and North-Eastern Africa, is particularly rich in long-awned hulled forms. The other, centering in China, Japan, and Tibet, is the source of hull-less short-awned, awnless or hooded types (Weaver, 1950; Smith, 1951).

Ethiopia, being one of the centers of genetic diversity for barley, has provided valuable sources of germplasm to the world. Large number of barley collections from Ethiopia are maintained in the United States and in other countries. These collections have been tested for their reactions to several plant pathogens (Moseman, 1971). The results from tests of collections of barley cultivars from Ethiopia, maintained by the United States Department of Agriculture, show that there are entries in the collections with genes for

resistance to many different pathogens. Schaller et al. (1963) found that, in the World Collection of 6689 entries, 113 of the 117 entries resistant to barley yellow dwarf virus were introductions from Ethiopia. In tests conducted with a field strain of barley stripe mosaic virus, Timian and Sisler (1955) found that four entries introduced from Ethiopia were outstanding for resistance to the virus. Metcalf and Johnston (1963) reported several introductions from Ethiopia to be resistant to *Ustilago nuda*. Qualset and Moseman (1966) compiled a report that many entries among 654 barley introductions from Ethiopia were found to be resistant to infection with cultures of *Erysiphe graminis, Ustilago nuda,* BYDV, BSMV, *Puccinia hordei, Pyrenophora teres, Septoria passerinii*, and *Rhynchosporium secalis*. Webster et al. (1980) identified 22 entries from Ethiopia resistant to barley scald in their evaluation of 18,000 entries from the USDA World Barley Collection.

Barley and its pathogens have co-existed for many centuries. *Rhynchosporium secalis* (Oud.) J. J. Davis, the causal organism of barley scald, is one of the pathogens threatening barley production in cool, humid areas of the world. Schaller (1951) reported losses in grain yields as high as 35 percent in California, and Ali et al. (1976) yield losses of 70 percent in Australia due to barley scald. Losses of up to 35 percent have been reported in Great Britain (Jenkins and Jemmett, 1967). Yield losses of 1-10 percent are not uncommon in many countries (Evans, 1969; Jenkins and Jemmett, 1967).

Resistance to *Rhynchosporium secalis* in barley has been reported on several occasions (Hansen and Magnus, 1973; Jenkins and Jemmett, 1967; Moseman, 1956; Reed, 1957; Riddle and Suneson, 1948; Roane and Starling, 1952; Rodriguez, 1948; Sarasola and Campi, 1947; Schein, 1960; Skoropad, 1960; Webster et al., 1980), but inheritance of resistance has been studied in relatively few cultivars (Baker and Larter, 1963; Bryner, 1957; Dyck and Schaller, 1961; Frecha, 1967; Habgood and Hayes, 1971; Riddle and Briggs, 1950; Starling et al., 1971; Wells and Skoropad, 1963). In these studies, 17 genes for resistance to

various isolates of *R. secalis* were identified. Starling et al. (1971) expressed doubt as to whether the number of gene loci identified was as large as reported in the literature.

Due to the appearance of new races or shifts in the pathogen populations, identification of potentially new sources of resistance genes to control barley scald disease appears to be a pertinent step. A notable example is the case of Atlas 46 in U.S.A. Atlas 46, having Rh2 and Rh3 resistance genes (Dyck and Schaller, 1961), was released in 1947 as resistant to California races of *R. secalis*, but by 1956 it was completely susceptible.

With the discovery of resistant Ethiopian barley cultivars from the USDA world barley collections, it seemed very desirable to study the inheritance of resistance in these cultivars to scald. The objectives of this research were to: (1) determine the number of gene loci conditioning resistance to barley scald in several Ethiopian barley cultivars, and (2) relate their genes to some of those previously reported.

CHAPTER 2

LITERATURE REVIEW

The Pathogen: *Rhynchosporium secalis* (Oud.) Davis

Mycological History and Taxonomy

The first preserved sample of *Rhynchosporium secalis* was collected in Norway in 1880 (Shipton et al., 1974) and identified as *Helminthosporium gramineum*. Oudemans (1897) made a collection in the Netherlands on rye and he described and named the pathogen *Marsonia secalis* (Oud.). The organism was isolated in Germany on both barley and rye in 1897 and was named *Rhynchosporium graminicola* Hein. (Frank, 1897). Later, Davis, in the United States, proposed the name *Rhynchosporium secalis* (Oud.) Davis in 1921 and the description of the genus was amended by both Davis (1921) and Caldwell (1937).

The genus *Rhynchosporium* belongs to the division Deuteromycotina, class Deuteromycetes, Order Moniliales, and family Moniliaceae.

The mycelium of the fungus is hyaline to light gray and the conidia are hyaline, one-septate, cylindrical to ovate with a short apical beak on most spores, and measure 12-20 by 2-4 microns (Dickson, 1956).

Variability of the Fungus

Heinsen (1901) found that isolates of *Rhynchosporium secalis* sporulated abundantly on some media, but were highly mycelial on others. Caldwell (1937), after culturing nine monoconidial isolates from barley on various media, concluded that the volume of mycelium and abundance of conidia varied directly with the concentration of dextrose or soluble carbohydrate present. Schein and Kerelo (1956) found that media without sugar allow

greatest sporulation and sucrose in the medium allows more sporulation than dextrose. They reported sporulation of the fungus to be practically nil on potato-dextrose agar and very high on lima-bean agar. The isolates grown on lima-bean agar had a pink color quite in contrast to the brown and black colonies on other media they used.

Despite the apparent absence of a sexual state, the fungus is capable of pathogenic variation. Habgood (1973) examined variation in aggressiveness and in conidial production in vitro in a number of single-spore isolates collected from within a single naturally infected plot of barley. Aggressiveness varied significantly both between lesions in the plot, and between isolates. He concluded that conidial production is not under nuclear control. He related *Rhynchosporium secalis* to *Phytophthora infestans* in which an extra-nuclear basis for some of the variability has also been suggested.

Sarasola and Campi (1947) reported that several barley varieties resistant to barley scald in the U.S. were susceptible in Argentina. Reed (1957) observed many mutants in cultures of most collections he made. He noted extreme variation in cultural characteristics between the mutant cultures, and between the mutants, and the original isolates he used. He compared fifteen different mutants and the parent monoconidial cultures for relative pathogenicity on four different barley varieties. A majority of the mutants were non-pathogenic. Williams and Owen (1975) observed significant differences in aggressiveness among United Kingdom isolates of the fungus.

The existence of physiologic races of *Rhynchosporium secalis* has been claimed by several workers (Ayesu-Offei, 1971; Dodoff, 1963; Dyck and Schaller, 1961a; Houston and Ashworth, 1957; Jackson and Webster, 1975; Reed, 1957; Sarasola and Campi, 1947; Schein, 1957). Riddle and Suneson (1948) found no good evidence of physiologic races in field trials conducted in California. Skoropad (1960) did not find any clear evidence of pathogenic races among the fifteen isolates tested on twenty-two differential barley varieties in Canada. Jackson and Webster (1975) studied pathogenic variability of *R. secalis* in

California and differentiated one hundred seventy-five single-spore isolates into seventy-five pathogenic races on 14 barley cultivars having many of the known genes for resistance to barley scald.

Evans and Griffiths (1971) observed a substantial decline in virulence of some isolates after frequent subculturing. They maintained virulence by inoculating isolates onto barley at intervals of three months and reisolating.

Host Range

Rhynchosporium secalis has been isolated from a number of grass genera and symptoms have been induced on an extensive range. The organism has been isolated from *Agropyron ciliare, A. semicostatum, A. repens, Bromus inermis, Elymus canadensis, Holcus lanatus, Hordeum jubatum, H. leporinum, H. murinum, H. vulgare, Lolium multiflorum, L. perenne, Phalaris arundinaceae, Secale cereale*, and several other grasses (Ali, 1972; Bartels, 1928; Caldwell, 1937; Dodoff, 1963; Kajiwara and Iwata, Owen, 1958; Ozoe, 1956; Sarasola and Campi, 1947; Schein, 1958, 1960; Smith, 1937). Results of cross inoculation tests carried out with isolates of *R. secalis* from different hosts indicate that not all isolates infect barley nor are all possible grass hosts affected by all isolates.

Survival and Dissemination

Survival of the fungus has been studied both in the laboratory and under field conditions (Caldwell, 1937; Evans, 1969; Ozoe, 1956; Skoropad, 1966). It has been reported that *R. secalis* persists from season to season as mycelium in barley debris. If the first leaf of a seedling emerges close to infected debris, disease symptoms appear in a fortnight under favorable conditions. Evans (1969) found that spring barley could become infected with *R. secalis* from the previous season's barley debris, even though attempts were made to bury all sources of inoculum by ploughing. He also has shown that the extent and

severity of the disease depends on the amount of stubble debris on the soil surface. When cool, moist conditions prevail, conidia are produced on the superficial stromata present on infected plant debris. Either free moisture or a high relative humidity (95-98 percent) is necessary for conidial production (Ayesu-Offei and Carter, 1971; Caldwell, 1937; Ozoe, 1956; Skoropad, 1962b). Sporulation can take place over a wide range of temperature, but abundant conidia are produced in the range 10-20 C within 24 hours (Caldwell, 1937; Owen, 1958; Skoropad, 1962b). The fungus loses its sporulating ability within 32 and 16 days at 10 and 18 C, respectively, when infected plant debris is kept continuously wet on a soil surface in the laboratory. Skoropad (1966) was able to demonstrate sporulation of the organism after 340 days following storage of infected debris in bags in the field. He also reported that production of successive batches of conidia in the presence of free moisture, and invasion by microbial saprophytes, destroyed the sporulating ability of the scald lesions, and that the most rapid deterioration of stromata occurred at 18 C in continually moist conditions on leaves in contact with the soil. Several (5-8) wetting and drying cycles deplete the reserves of the fungus so that sporulation ceases even under optimum conditions (Skoropad, 1962b). Bartels (1928) in his investigation on survival of the fungus under field conditions found viability to be maintained for 6-9 months. Ozoe (1956) found that the fungus survived for about one year on infected straw kept in the laboratory. He noted that it usually failed to oversummer if the straw was left in the open field or buried in the soil. Polley (1971) thinks that, sclerotia, which give rise to hyphae and conidia on the return of favorable conditions, are means of overwintering in Great Britain. In Australia, it has been demonstrated that the fungus survived in the field in infected debris and could give rise to infection for up to eight months (Shipton et al., 1974).

It has been claimed earlier that the fungus is soil-borne (Bartels, 1928; Heinsen, 1901; Mackie, 1929). However, there is no substantial piece of evidence that the fungus actually

survives saprophytically in the soil (Brooks, 1928; Caldwell, 1937; Ozoe, 1956; Skoropad, 1962b). Seeds have also been shown to carry the fungus and are particularly important in long-range dissemination of the organism (Habgood, 1971; Ozoe, 1956; Skoropad, 1959; Smith, 1937). Coleoptiles are attacked when germination of infected seeds takes place under conditions favorable to the pathogen (Skoropad, 1959). Volunteer barley plants growing from grain shed before and during harvesting become infected with *R. secalis* when spores are dispersed from the stubble (Evans, 1969; Skoropad, 1960).

Ozoe (1956) and Skoropad (1960) have suggested that after development of the first lesions, secondary inoculum is dispersed by wind-borne rain splash. Ozoe (1956) claimed that the number of conidia in the air appeared to be greater in the day than at night. However, Ayesu-Offei and Carter (1971) reported that conidia may be released at any time of the day or night. Skoropad (1959) reported that conidia were most abundant during rainstorms and that they were usually trapped in clusters of three to ten, which indicated that they were transported in droplets of water.

Field observations have shown that a low level of primary infection can give rise to a severe epidemic if subsequent weather conditions are favorable for secondary infection (Jenkins and Jemmett, 1967). Skoropad (1960) has emphasized that cool, moist conditions are necessary for the establishment of the disease in Canada, whereas Ozoe (1956) reported that a warm winter with heavy rains caused more serious infection than occurred in normal years in Japan.

Ayesu-Offei and Carter (1971) found that sporulation occurred most abundantly when free water was available and that conidia were released simultaneously with rainfall or irrigation. Their experiments have shown that the conidia are not readily dislodged by wind alone, supporting the view that release and dispersal of the conidia are mainly the result of water splash. The maximum number of airborne conidia they trapped in a day was 272 which is very small compared with numbers of spores of other pathogens trapped

within cereal crops by other researchers. Hirst (1961) reported catches of up to 11,000 uredinospores of *Puccinia graminis* per cu m air in infected spring wheat, and Sreeramulu (1962) mentioned concentrations of as high as 14,300 chlamydospores of *Ustilago nuda* per cu m air over barley infected with the fungus. Stedman (1980) showed that the number of spores trapped was not related to the quantity of or duration of rainfall but was related to the mean rate of fall during brief showers only. He reported catches of up to 436 spores per cu m, most spores being trapped at ground level.

Conidia Germination and Infection Process

Conidia can germinate readily in water from one or both cells within 12 hours at 15 C. More than one germ tube may arise from either cell which may branch (Ayesu-Offei and Clare, 1970; Caldwell, 1937; Smith, 1937; Kelemu and Sharp, unpublished). Ayesu-Offei (1971) found germination continued on leaf surfaces for a number of days. A portion of germ tubes develop appressoria, which may develop either at the tips of germ tubes or be sessile on the conidia. Ayesu-Offei and Clare (1970) observed penetration occurred within 24 hours even in the absence of appressorial formation. These authors confirmed Caldwell's (1937) observation that penetration occurs directly and not through the stomata as reported by Bartels (1928) and Mackie (1929). They demonstrated that hyphae below the appressoria penetrated the cuticle and extensive mycelial mats were formed between the cuticle and the outer epidermal cell walls. Epidermal cell walls beneath the subcuticular hyphae became swollen and collapsed. Mesophyll cells, beneath the subcuticular hyphae, also collapsed and died before being entered by hyphae which penetrated between epidermal cells. These workers indicated that penetration of the cuticle and collapse of the epidermal cell walls and mesophyll cells was due to the activity of materials excreted by the fungus.

The Environment

Disease symptom expression and the rate of symptom development are determined by host and pathogen genotypes and the existing environmental conditions. Phenotypic variability of the complex interaction involved complicates the genetic inferences that have to be made. Genetic factors cannot cause a character to develop unless they have the proper environment, and, conversely, no amount of manipulation of the environment will cause a character to develop unless the necessary genetic factors are present. Environment plays a role in contributing variability among individuals. Distinguishing among genotypes on phenotypic grounds is facilitated if the environmental component of variability is reduced. An appreciation is thus necessary of the non-genetic factors contributing to phenotypic variability of disease symptom expression.

Temperature and Moisture

Moisture is essential for the production of inocula. The atmosphere must be humid enough for the tissue to absorb moisture (Caldwell, 1937; Ozoe, 1956; Skoropad, 1966). Production of conidia is favored by temperatures between 10 and 20 C (Ozoe, 1956; Skoropad, 1957, 1960, 1962b). The period of time during which *R. secalis* retains its ability to sporulate in lesions of naturally infected barley leaves is strongly influenced by an interrelationship of moisture, temperature, and location of leaves in relation to the soil. Conidial production ceases during a dry period and a new crop is produced when the stroma is wet again.

Optimum infection occurs at a soil temperature of 16 C; it decreases sharply at 20 C, and is almost absent at 22 C. Lesion development proceeds normally when the post-inoculation temperature is 12-24 C, but few lesions develop and development is slow when the

post-inoculation conditions are 6-12 C or above 24 C; exposure to lower temperature initially followed by exposure to higher temperature favors lesion development (Caldwell, 1937; Skoropad, 1957).

Ali (1972) showed that the effect of temperature on symptom expression is subject to the particular combination of isolate and host genotypes examined. He observed that at high diurnal temperature regimes (18 C min./30 C max.), the ability of certain isolates to infect hosts normally susceptible to them was greatly impaired, while other isolates could infect hosts normally resistant to them. It was observed that at low temperature regimes (8 C min./20 C max.) the rate of symptom development proceeded most rapidly for certain isolates whilst higher temperatures (15 C min./24 C max.) favored the rate of symptom development of others. Evidence was also found to indicate that variability in the pathogenic characteristics of isolates may likewise be differentially influenced by environmental modification.

Nutrition

The effect of mineral nutrition on disease severity is largely unknown. Vandervalk (1942), as cited by Shipton et al. (1974), reported that the disease disappeared following cultivation and the application of nitrate. The disappearance of the disease, however, may be attributed to the destruction of much of the inoculum by cultivation. Jenkins and Jemmett (1967) occasionally found higher levels of disease in some variety trial plots receiving higher levels of nitrogen. According to the report by Ozoe (1956) inorganic nitrogen sources enhance susceptibility to disease.

Experiments conducted by Jenkyn and Griffiths (1976) showed that nitrogen fertilizer did decrease number of infections which contrasts with field observations that crops receiving most nitrogen are usually more severely diseased (Doling, 1964). The increased disease in the field may have to be attributed to enhanced lesion development or sporulation

rather than increased infection. Jenkyn and Griffiths (1978) found the susceptibility of cultivars to barley scald negatively correlated with water-soluble carbohydrate content and positively with nitrogen content.

Interaction: Host, Pathogen and Environment

Symptoms

The disease of barley caused by *Rhynchosporium secalis* is commonly referred to as *Rhynchosporium* leaf blotch, barley leaf blotch, *Rhynchosporium* scald, or simply scald. Symptoms produced on barley are usually distinctive for the pathogen on that host. Lesions on naturally or artificially infected leaves begin as grey, water soaked areas 8-14 days after inoculation. At this stage, lesions dry out but retain a grey-green color which persists even when the uninfected parts of a leaf have become straw colored. Usually the lesions become oval-shaped with dry, pale-brown or white centers surrounded by dark-brown margins. Leaves of a susceptible seedling barley cultivar completely wilt and show no discrete lesions after infection by the pathogen. Barley scald symptoms can appear on leaf sheaths, floral bracts, pericarp and awns of barley.

Genetics of Scald Resistance

Mackie (1929) was the first to study the inheritance of scald resistance. He found that resistance in an unnamed barley variety was governed by a single recessive gene. Twenty years later Riddle and Briggs (1950) identified a single dominant gene controlling resistance in La Mesita (CI. 7565), which was also present with a recessive gene in its derivatives, Trebi (CI. 936) and Modoc (CI. 7566) and with one or more additional dominant genes in Turk (CI. 14400). Bryner (1957) reported that resistance in Brier (CI. 7157) was conferred by a single dominant gene. Bryner (1957) was the first to use a designation for genes conferring resistance to *R. secalis*. He assigned the symbol Rha (later amended to Rh) to the dominant gene he found in Brier.

Of the several studies made on the genetics of scald resistance, that of Dyck and Schaller (1961) is the most extensive. Using four pathogenic races of *R. secalis*, they identified five dominant genes for resistance in eight varieties of barley which they designated Rh2 to Rh5. The varieties Atlas and Atlas 46 possessed the Rh2 gene which conditioned a type 1 reaction to race U.S.1 and a type 2 reaction to U.S.7 of *R. secalis*. Atlas 46 had the Rh3 gene, in addition to the Rh2 gene, which conditioned a type 0 reaction to races U.S.1, U.S.7, and U.S.8. The same gene was found in the varieties Turk and possibly Brier. Rh4 gene was reported to condition resistance of La Mesita, Trebi and Osiris (CI. 1622). Rh4 gene was closely linked with the Rh3 gene, with a recombination value of 1.0±0.78 percent. An allele at the Rh4 locus, $Rh4^2$ gene was identified in Modoc. Rh5 gene, which was independent of the Rh3 and Rh4 genes, was present in Turk. These genes were demonstrated to be specific against the races of the pathogen used. In subsequent years, Baker and Larter (1963) studied the inheritance of resistance to a Saskatchewan isolate of the pathogen in five varieties of barley. They found a pair of complementary recessive genes, rh6 and rh7, in Jet (CI. 967) and Steudelli (CI. 2266), and an incompletely dominant gene, Rh9, in Kitchin (CI. 1296) and Abyssinian (CI. 668). They confirmed the presence of a single dominant gene for resistance in Turk. The effectiveness of the two complementary recessive genes for resistance was impaired by temperatures above 25 C during the infection period.

Wells and Skoropad (1963) used an Alberta isolate of *R. secalis* to determine the mode of inheritance of resistance in eight resistant barley cultivars. They found that seven of the cultivars, Turk, Bey, Rivale (CAN. 258), 36Ab1991 (CAN. 136), CI. 3515, CI. 8256 and Osiris, possessed in common a dominant gene considered to be Rh3. A recessive gene, which they designated rh8, governed resistance in Nigrinudum (CI. 2222). In 1967 Frecha reported that Osiris, Psaknon and Atlas 46 had a dominant gene for scald resistance in common, and that Atlas 46 had also an additional dominant gene.

Starling et al. (1971) recognized the predominance of the Rh-Rh3-Rh4 complex locus in the barley cultivars they studied. The results indicated that Atlas 46, Turk, Brier, La Mesita, Modoc, Gembloux 14, Alask (CI. 534 and CI. 4106), Tennessee Winter (CI. 876), Kentucky No. 36, Olympia, Tschermak, Hudson, Carstens 2-row, CI. 3515, CI. 8071, CI. 8101, CI. 8256, CI. 9042 and CI. 10176 all had a single gene or gene locus in common. CI. 8618 was found to have a dominant gene not found in any other variety they tested. Atlas 46 had an additional gene which was also present in Atlas, and CI. 3515 also had an additional dominant gene, different from that in Atlas. Evans (1969) detected a dominant gene for resistance in Atlas 46, Turk and Osiris. These genes were presumed to be Rh3 in Atlas 46 and Turk and Rh4 in Osiris since they were either allelic or closely linked.

Habgood and Hayes (1971) studied the inheritance of resistance to three isolates of *R. secalis* in 18 barley varieties. The results of their experiment suggested that the resistance genes in Turk, Atlas 46, Brier, Modoc and Cb 1084 are all situated at the same locus even though separate loci up to 1.7 cross-over units apart could give the same results. A less conclusive evidence was obtained that Hudson (CI. 8067) and Dea also contained genes at this locus. They further differentiated the gene in Modoc from the others at the same locus by its ineffectiveness against one of the isolates used and that in Cb 1084 by its incomplete dominance. The inheritance of resistance in CI. 3515, CI. 8256, Gembloux 14 and La Mesita was reported to be identical to that in Osiris. It was confirmed that resistance in Jet was controlled by two complementary recessive genes, but one of these was shown to be situated at the locus carrying the dominant genes in Osiris, Brier, Turk and Modoc. A recessive gene for resistance was found in CI. 4364 and CI. 4368 which has not been previously reported. Bockelman et al. (1977), using trisomic analysis, determined chromosomal location of the resistance genes in Kitchin and in Jet. They showed that Kitchin possessed a single gene, Rh9, on chromosome 4, whereas, Jet contained rh7 and rh6 on chromosomes 3 and 4, respectively.

Habgood and Hayes (1971), aided by their discovery that a single gene segregation apparent after a 14-day incubation period might be interpreted as the action of two complementary genes if re-examined after a 28-day incubation period, have detected a gene in Osiris which is complementary to the one effective 14 days after inoculation. This gene has not been previously reported since its effect is not apparent until well after the normal times of assessment. The symbol Rh10 was suggested for this gene whereas rh11 was proposed for the recessive gene in CI. 4364 and CI. 4368. These workers further proposed revised symbols for the designation of some of the resistance genes identified. Summarizing the results obtained by Habgood and Hayes (1971), there are five alleles at the Rh locus, two are dominant (Rh and Rh^2), two are incompletely dominant (Rh^3 and Rh^4) and one is recessive (rh^5).

According to studies by Ali (1972), environmental conditions of testing have considerable influence on symptom expression and thus upon interpretation of genetic results. Transgressive segregation for increased scald resistance has been indicated by Ali. Habgood (1972) detected a high level of field resistance at the adult stage which escaped detection in routine seedling inoculation studies. Quantitative differences between various barley cultivars in resistance to *R. secalis* at the seedling stage have been demonstrated by Jenkyn (1969), Williams (1969), Fowler and Owen (1971), Evans and Griffiths (1971) and Habgood (1972). Habgood (1974) studied the inheritance of partial resistance, which appears to be race non-specific, in European spring barley cultivars. He reported that resistance was complex in inheritance, the results being incompatible with any hypothesis involving less than four genes and that transgressive segregation occurred in all cross combinations in the F_3 material.

Fowler and Owen (1971) studied the mechanism of resistance to barley scald. Their report indicated that the earliest point at which resistance was expressed was at penetration of the cuticle. Host resistance did not affect germination or appressoria formation (Ayres and Owen, 1970; Kelemu and Sharp, unpublished).

CHAPTER 3

MATERIALS AND METHODS

Ethiopian barleys which had shown consistent and uniform resistance to isolates of *R. secalis* in both field and greenhouse tests were studied to determine the number of loci for genes conditioning resistance to several isolates of the pathogen. Each of the five Ethiopian barley cultivars chosen was crossed with Betzes, a susceptible barley variety to all of the isolates used, to determine the number of genes for resistance to barley scald in each; and all five were crossed in all possible combinations with each other to determine whether any had genes for resistance at common loci or linked. Each of these barleys was also crossed with twelve barley cultivars which had previously been studied for inheritance of reaction to *R. secalis* and assigned gene symbols. The F_1's from crosses between Ethiopian barleys and Betzes were backcrossed to Betzes. The cultivars used as parents in this investigation are listed in the Appendix, Table 19, with their origin and some agronomic characters.

Seven different isolates of the fungus from five countries were used in the experiment. Two isolates of the pathogen were from Ethiopia (Debre Zeit and Holetta areas), two from U.S.A. (California and Montana), one from Tunisia (Beja), one from Morocco (Beni-Mellal), and one from Mexico (El Batan). The isolates have been given the designation Eth-DZ-83, Eth-HT-83, US-CA-83, US-MT-83, Tun-BJ-81, Mor-BM-77, Mex-EB-83, indicating the country, the particular place and year of collection, respectively. The fungus was isolated from infected barley leaves using the method described by Schein and Kerelo (1956). The spores of the different isolates were lyophilized and kept in a refrigerator as a safeguard if attenuation of the isolates occurred in the process of subculturing.

The genetic analyses were made on the basis of F_1, BC_1, F_2 populations and some F_3 families. At least 200 seeds of F_2 populations of each cross were grown in metal flats (14" × 10" × 3") at the same time as the parents, F_1 and backcrosses to the susceptible parent in some cases. Betzes was included as a susceptible check in each flat. Sixteen F_3 lines, each line containing at least 30 seeds, were planted in one flat. The F_3 lines were separated from one another using pieces of cardboard. Parental cultivars were planted with their F_3 populations. All flats were kept in the greenhouse maintained at about 21 C prior to inoculations. In some warm days the temperature had risen above 26 C.

To prepare inoculum, conidia from lyophilized cultures were transferred to Petri dishes containing fresh lima bean agar and were kept in a constant temperature cabinet at 18 C. Plantings of barley and transfers of isolates were usually made the same day. A spore suspension, harvested from two week old cultures by adding distilled water and rubbing the colonies off with a glass slide, was used as inoculum. The suspension of spores and agar was filtered through four layers of cheesecloth to remove the agar fragments. Inoculations were made 14 days after planting. The spore suspension with a concentration of at least 100,000 spores per ml was applied using a spray bottle until wetness. The plants were then incubated in the dark for 24 hours at 100 percent relative humidity (21 C) and subsequently transferred to a growth chamber maintained at alternating temperatures of 21 C (light) and 16 C (dark). In 10-14 days the scald symptoms developed sufficiently for evaluation. The scale of 0 to 4, described by Dyck and Schaller (1961), was used in evaluating the reaction of individual plants (0 = no lesions, a fully resistant reaction; 1 = small lesions on the margin of the second leaf only; 2 = somewhat larger lesions on the margin of the second leaf and a large lesion at the base of the leaf or at the lower extent of the leaf area exposed when inoculated, but no lesions on the first leaf; 3 = large lesions covering almost the entire second leaf, occasionally causing the leaf to collapse and/or wilt, with a few small lesions on the first leaf; 4 = all exposed areas, both first and second leaf, wilted with no

definite lesions). Plants with 0 and 1 reactions (resistant) and those with 3 and 4 reactions (susceptible) were grouped for convenience in presenting the data. Intermediate plants (type 2 reaction) were observed only in crosses involving Kitchin, Atlas and Atlas 46. F_3 lines were classed as resistant, segregating, or susceptible. Scald reactions of the plants in each segregating F_3 line were classified using the scale of 0 to 4.

Parental cultivars and their F_2 populations were space planted at the Horticultural Farm, Bozeman, Montana on May 16 and 17 in 1984.

A spore/agar suspension was prepared by blending two-week-old cultures in distilled water (cultures from 10 Petri dishes (100 mm × 15 mm) in 1 liter of distilled water). Tillering plants were inoculated with US-MT-83 isolate of *R. secalis* twice at a weekly interval in later afternoons in June using a sprayer. All materials were sprinkler irrigated for a few minutes before inoculations. Immediately after inoculation, the plants were covered with plastic sheets for about 14 hours to create a favorable environment for infection. Scald readings were made in July using a modified 0 to 4 scale, where class 1 was modified to include plants with small lesions on the margin of the second leaves and/or lesions on leaf sheaths.

The probability values for goodness of fit to expected ratios were calculated using the Chi square method. The maximum recombination frequency which could have passed undetected was calculated using the formula outlined by Hanson (1959): $Prc = 1 - \sqrt[n]{0.05}$, where n is the number of F_2 plants or F_3 lines used, and Prc is the proportion of detectable recombinants.

CHAPTER 4

RESULTS

The seedling reactions of 18 barley cultivars to seven isolates of *R. secalis* are shown in Table 1. Tun-BJ-81 isolate was found to be the most virulent attacking 14 of the parents, whereas US-MT-83 was the least virulent infecting only one, Betzes. The more avirulent isolate will detect the largest number of resistance genes, hence, US-MT-83 was used to detect resistance genes in most instances. PI. 382488, PI. 383036 and Osiris were resistant to all of the seven isolates. PI. 382282, PI. 382471 and PI. 382509 reacted identically to all of the isolates.

There could be several pairs of cultivars whose resistances when combined would, at least theoretically, be effective against all of the isolates used in this study if the resistance of the cultivars can be combined readily. Even though PI. 382488 was resistant to all of the isolates in this study at normal temperature regime, temperatures greater than 26 C induced a susceptible reaction to isolates Tun-BJ-81, Eth-HT-83, Mex-EB-83 and Mor-BM-77. The resistance in PI. 382282 was also impaired by temperatures above 26 C to Mor-BM-77 and Eth-HT-83 isolates.

Scald lesions were observed on leaf sheaths of PI. 382282, PI. 382472, PI. 382488, PI. 382509 and PI. 383036 in the field, whereas, the leaves remained free of symptoms. Brown discoloration and subsequent wilting of leaf sheaths of these cultivars was also noted in seedling tests in growth chambers while the leaves were resistant to the isolates shown in Table 1. Both the leaf sheaths and leaves of Osiris were symptomless, whereas, those of Betzes were susceptible. Leaf sheath resistance and leaf susceptibility were noted in other

Table 1. Barley Cultivars Used and Their Reactions to Seven Isolates of *Rhynchosporium secalis*.

Cultivar			Isolates						
P.I.	Name	C.I.	US-MT-83	US-CA-83	Eth-DZ-83	Eth-HT-83	Tun-BJ-81	Mex-EB-83	Mor-BM-77
382282			R	R	S	R*	S	R	R*
382471			R	R	S	R	S	R	R
382488			R	R	R	R*	R*	R*	R*
382509			R	R	S	R	S	R	R
383036			R	R	R	R	R	R	R
	Betzes	6398	S	S	S	S	S	S	S
	Brier	7157	R	S	S	S	S	R	R
	Abyssinian	3940	R	R	S	S	S	R	R
	Atlas	4118	R	S	R	R	S	S	S
	Atlas 46	7323	R	S	R	R	S	R	R
	Turk	14400	R	S	R	R	S	R	R
	Osiris	1622	R	R	R	R	R	R	R
	La Mesita	7565	R	S	R	R	S	R	R
	Trebi	936	R	S	R	R	S	R	S
	Modoc	7566	R	S	R	R	S	R	R
	Jet	967	R*	S	R	R	S	S	S
	Nigrinudum	2222	R	S	R	R	R	S	S
	Kitchin	1296	R	S	R	R	S	S	S

*Susceptible at temperatures above 26 C.

cases. This phenomenon has apparently been overlooked and previously unreported. Some barley cultivars have resistant leaf sheaths and susceptible leaves or vice versa to powdery mildew (*Erysiphe graminis* f. sp. *hordei*) (Moseman, personal communication).

Cultivars Modoc, Jet, Nigrinudum, La Mesita and Trebi were susceptible to US-MT-83 isolate in the field (Appendix, Table 17). Habgood and Hayes (1971) reported that La Mesita developed disease symptoms in the field. Riddle and Briggs (1950) concluded that susceptibility in adult and seedling plants of La Mesita is associated with senescence of the leaves. The fact that Jet has temperature sensitive resistance genes may explain its susceptibility in the field.

Segregation in Resistant × Susceptible Crosses

Segregation results of the progeny from crosses involving resistant cultivars and susceptible Betzes in response to inoculation with the different isolates are presented in Table 2.

PI. 382282

Although PI. 382282 was susceptible to isolates Eth-DZ-83 and Tun-BJ-81, it was found to be resistant to US-MT-83, US-CA-83, Eth-HT-83 (at lower temperatures) and Mor-BM-77 (at lower temperatures) (Table 1). In the cross with Betzes which is susceptible to all isolates, a test of F_2 progeny to US-MT-83 gave a good fit to a 9:7 ratio (Table 2). The F_1 when backcrossed to the susceptible parent showed a good fit for a ratio of one resistant to three susceptible. Furthermore, the segregation in the F_3 gave a good fit to a ratio of 1 resistant:8 segregating:7 susceptible families, with a ratio of 3 resistant:1 susceptible or 9 resistant:7 susceptible plants in the segregating families. The F_1 plants from this cross were resistant. These results suggest that the resistance to US-MT-83 in PI. 382282 is controlled by two complementary dominant genes.

Table 2. The Reaction of Seedling Progeny from Crosses Involving Betzes to Isolates of *Rhynchosporium secalis*.

Cross	Generation	Isolate	Observed Frequency			Ratio	Probability
			Res.	Segr.	Susc.		
PI. 382282 × Betzes	F_2	US-MT-83	126	–	105	9:7	.65
PI. 382282 × Betzes	F_1	US-MT-83	8	–	–		
PI. 382282 × Betzes/Betzes	BC_1	US-MT-83	9	–	22	1:3	.76
PI. 382282 × Betzes	F_3	US-MT-83	3	13	16	1:8:7	.51
PI. 382282 × Betzes	F_2	US-CA-83	203	–	63	3:1	.67
PI. 382282 × Betzes	F_1	US-CA-83	3	–	–		
PI. 382282 × Betzes/Betzes	BC_1	US-CA-83	7	–	8	1:1	1.0
PI. 382282 × Betzes	F_3	US-CA-83	7	16	9	1:2:1	.88
PI. 382282 × Betzes	F_2	Mor-BM-77	30	–	72	1:3	.36
PI. 382282 × Betzes	F_1	Mor-BM-77	–	–	4		
PI. 382282 × Betzes/Betzes	BC_1	Mor-BM-77	–	–	10	0:1	1.0
PI. 382282 × Betzes	F_3	Mor-BM-77	10	10	12	1:2:1	.09
PI. 382282 × Betzes	F_2	Mex-EB-83	35	–	126	1:3	.39
PI. 382282 × Betzes	F_1	Mex-EB-83	–	–	5		
PI. 382282 × Betzes	F_3	Mex-EB-83	9	13	10	1:2:1	.56
PI. 382471 × Betzes	F_2	US-MT-83	106	–	46	3:1	.16
PI. 382471 × Betzes	F_1	US-MT-83	5	–	–		
PI. 382471 × Betzes/Betzes	BC_1	US-MT-83	11	–	15	1:1	.56
PI. 382471 × Betzes	F_3	US-MT-83	5	11	16	1:2:1	.005
PI. 382471 × Betzes	F_2	US-CA-83	149	–	67	3:1	.002
PI. 382471 × Betzes	F_1	US-CA-83	4	–	–		
PI. 382471 × Betzes/Betzes	BC_1	US-CA-83	13		12	1:1	1.0
PI. 382471 × Betzes	F_3	US-CA-83	10	10	12	1:2:1	.09
PI. 382471 × Betzes	F_2	Mor-BM-77	38	–	100	1:3	.56
PI. 382471 × Betzes	F_1	Mor-BM-77	–	–	5		
PI. 382471 × Betzes	F_3	Mor-BM-77	6	16	10	1:2:1	.61
PI. 382471 × Betzes	F_2	Mex-EB-83	75	–	31	3:1	.37
PI. 382471 × Betzes	F_1	Mex-EB-83	3	–	–		
PI. 382471 × Betzes/Betzes	BC_1	Mex-EB-83	14	–	13	1:1	1.0

Table 2 (continued).

Cross	Generation	Isolate	Observed Frequency			Ratio	Probability
			Res.	Segr.	Susc.		
PI. 382471 × Betzes	F_3	Mex-EB-83	6	15	11	1:2:1	.43
PI. 382471 × Betzes	F_2	Eth-HT-83	46	–	101	1:3	.10
PI. 382471 × Betzes	F_1	Eth-HT-83	–	–	3		
PI. 382471 × Betzes/Betzes	BC_1	Eth-HT-83	–	–	7	0:1	1.0
PI. 382471 × Betzes	F_3	Eth-HT-83	3	9	4	1:2:1	.83
PI. 382488 × Betzes	F_2	US-MT-83	83	–	30	3:1	.79
PI. 382488 × Betzes	F_1	US-MT-83	3	–	–		
PI. 382488 × Betzes/Betzes	BC_1	US-MT-83	7	–	10	1:1	.63
PI. 382488 × Betzes	F_3	US-MT-83	7	12	13	1:2:1	.12
PI. 382488 × Betzes	F_2	US-CA-83	125	–	47	3:1	.54
PI. 382488 × Betzes	F_1	US-CA-83	3	–	–		
PI. 382488 × Betzes/Betzes	BC_1	US-CA-83	5	–	7	1:1	.77
PI. 382488 × Betzes	F_3	US-CA-83	6	14	12	1:2:1	.25
PI. 382488 × Betzes	F_2	Mor-BM-77	43	–	101	1:3	.21
PI. 382488 × Betzes	F_1	Mor-BM-77	–	–	2		
PI. 382488 × Betzes/Betzes	BC_1	Mor-BM-77	1		9	0:1	1.0
PI. 382488 × Betzes	F_3	Mor-BM-77	9	13	10	1:2:1	.56
PI. 382488 × Betzes	F_2	Eth-DZ-83	34	–	108	1:3	.85
PI. 382488 × Betzes	F_1	Eth-DZ-83	–	–	4		
PI. 382509 × Betzes	F_2	US-MT-83	103	–	88	9:7	.57
PI. 382509 × Betzes	F_1	US-MT-83	5	–	–		
PI. 382509 × Betzes/Betzes	BC_1	US-MT-83	5	–	7	1:3	.32
PI. 382509 × Betzes	F_3	US-MT-83	8	9	15	1:8:7	.00
PI. 382509 × Betzes	F_2	US-CA-83	152	–	46	3:1	.62
PI. 382509 × Betzes	F_1	US-CA-83	3	–	–		
PI. 382509 × Betzes/Betzes	BC_1	US-CA-83	5	–	5	1:1	1.0
PI. 382509 × Betzes	F_3	US-CA-83	8	11	13	1:2:1	.10
PI. 382509 × Betzes	F_2	Mex-EB-83	121	–	52	3:1	.15

Table 2 (continued).

Cross	Generation	Isolate	Observed Frequency			Ratio	Probability
			Res.	Segr.	Susc.		
PI. 382509 X Betzes	F_1	Mex-EB-83	3	–	–		
PI. 382509 X Betzes/Betzes	BC_1	Mex-EB-83	4	–	6	1:1	.75
PI. 382509 X Betzes	F_3	Mex-EB-83	8	10	14	1:2:1	.03
PI. 382509 X Betzes	F_2	Mor-BM-77	43	–	96	1:3	.13
PI. 382509 X Betzes	F_1	Mor-BM-77	–	–	3		
PI. 382509 X Betzes/Betzes	BC_1	Mor-BM-77	–	–	7	0:1	1.0
PI. 382509 X Betzes	F_3	Mor-BM-77	8	13	11	1:2:1	.43
PI. 382509 X Betzes	F_2	Eth-HT-83	130	–	49	3:1	.52
PI. 382509 X Betzes	F_1	Eth-HT-83	2	–	–		
PI. 382509 X Betzes/Betzes	BC_1	Eth-HT-83	6	–	9	1:1	.61
PI. 382509 X Betzes	F_3	Eth-HT-83	8	14	10	1:2:1	.69
Betzes X PI. 383036	F_2	US-MT-83	112	–	41	3:1	.67
Betzes X PI. 383036	F_1	US-MT-83	3	–	–		
Betzes X PI. 383036/Betzes	BC_1	US-MT-83	6	–	8	1:1	.79
Betzes X PI. 383036	F_3	US-MT-83	10	13	8	1:2:1	.59
Betzes X PI. 383036	F_2	US-CA-83	137	–	55	3:1	.28
Betzes X PI. 383036	F_1	US-CA-83	3	–	–		
Betzes X PI. 383036/Betzes	BC_1	US-CA-83	9	–	6	1:1	.61
Betzes X PI. 383036	F_3	US-CA-83	3	22	7	1:2:1	.06
Betzes X PI. 383036	F_2	Mex-EB-83	47	–	126	1:3	.57
Betzes X PI. 383036	F_1	Mex-EB-83	–	–	3		
Betzes X PI. 383036/Betzes	BC_1	Mex-EB-83	2	–	13	0:1	
Betzes X PI. 383036	F_3	Mex-EB-83	6	11	15	1:2:1	.02
Betzes X PI. 383036	F_2	Mor-BM-77	45	–	130	1:3	.90
Betzes X PI. 383036	F_1	Mor-BM-77	–	–	3		
Betzes X PI. 383036/Betzes	BC_1	Mor-BM-77	1	–	10	0:1	
Betzes X PI. 383036	F_3	Mor-BM-77	8	13	11	1:2:1	.43
Betzes X PI. 383036	F_2	Eth-HT-83	146	–	57	3:1	.35
Betzes X PI. 383036	F_1	Eth-HT-83	3	–	–		
Betzes X PI. 383036/Betzes	BC_1	Eth-HT-83	10	–	15	1:1	.42

Table 2 (continued).

Cross	Generation	Isolate	Observed Frequency			Ratio	Probability
			Res.	Segr.	Susc.		
Betzes X PI. 383036	F_3	Eth-HT-83	6	13	9	1:2:1	.68
Betzes X PI. 383036	F_2	Eth-DZ-83	38	–	131	1:3	.51
Betzes X PI. 383036	F_1	Eth-DZ-83	–	–	3		
Betzes X PI. 383036/Betzes	BC_1	Eth-DZ-83	–	–	12	0:1	1.0
Betzes X PI. 383036	F_3	Eth-DZ-83	5	19	7	1:2:1	.40
Betzes X PI. 383036	F_2	Tun-BJ-81	43	–	124	1:3	.89
Betzes X PI. 383036	F_1	Tun-BJ-81	–	–	3		
Betzes X PI. 383036	F_3	Tun-BJ-81	9	15	6	1:2:1	.75
Betzes X Brier	F_2	US-MT-83	367	–	121	3:1	.96
Betzes X CI. 3940	F_2	US-MT-83	151	–	45	3:1	.56
Atlas X Betzes	F_2	US-MT-83	133	–	41	3:1	.73
Atlas X Betzes	F_2	Eth-HT-83	33	–	15	3:1	.40
Atlas 46 X Betzes	F_2	US-MT-83	256	–	15	15:1	.72
Atlas 46 X Betzes	F_3	US-MT-83	8	17	0	7:8:1	.14
Turk X Betzes	F_2	US-MT-83	129	–	40	3:1	.76
Turk X Betzes	F_3	US-MT-83	8	11	6	1:2:1	.72
Osiris X Betzes	F_2	US-MT-83	155	–	7	15:1	.39
La Mesita X Betzes	F_2	US-MT-83	185	–	57	3:1	.66
La Mesita X Betzes	F_3	US-MT-83	8	13	4	1:2:1	.52
Trebi X Betzes	F_2	US-MT-83	150	–	50	3:1	1.0
Betzes X Modoc	F_2	US-MT-83	315	–	101	3:1	.98
Betzes X Modoc	F_2	Mor-BM-77	7	–	75	1:15	.53
Betzes X Jet	F_2	US-MT-83	80	–	119	7:9	.35
Betzes X Jet	F_2	Eth-DZ-83	15	–	54	1:3	.63
Nigrinudum X Betzes	F_2	US-MT-83	42	–	113	1:3	.61
Nigrinudum X Betzes	F_2	Eth-DZ-83	20	–	50	1:3	.58
Kitchin X Betzes	F_2	US-MT-83	69	–	18	3:1	.78

The F_2 population from the cross PI. 382282 X Betzes gave a different ratio with US-CA-83 isolate. Two hundred-sixty six F_2 plants segregated fitting a 3:1 ratio with this isolate. The backcross and F_3 populations gave a very good fit to a single gene hypothesis.

A single recessive gene was detected in PI. 382282 using Mor-BM-77 isolate. The F_3 families gave a poor fit to a 1:2:1 ratio. This could be due to the non-random selection of the F_3 samples. However, a ratio of 1 resistant:3 susceptible plants was obtained in all of the 10 segregating families. A similar ratio was obtained with Mex-EB-83 isolate. The reaction of the 32 individual F_3 lines, however, was not the same to the two isolates, which suggested that different genes could be involved.

PI. 382471

This cultivar was resistant to US-MT-83, US-CA-83, Eth-HT-83, Mex-EB-83 and Mor-BM-77 isolates.

When tested with the US-MT-83 isolate, the segregation of 152 F_2 plants from PI. 382471 X Betzes fitted a 3:1 ratio, indicating that a single dominant gene conditioned resistance of PI. 382471 to this isolate. The backcross gave a satisfactory fit to a 1:1 ratio, which supported the hypothesis that a single gene conditioned resistance in this interaction. Even though the 32 F_3 lines from this cross gave a poor fit to a 1:2:1 ratio, all of the 11 segregating lines segregated in a 3:1 ratio manner giving a further support for a single gene hypothesis. The F_2 populations from the same cross fitted poorly to a 3:1 ratio giving an excess of susceptible plants when tested with US-CA-83 isolate. However, the observed ratio more nearly approximated that expected from a single gene than from other gene combinations. Moreover, the backcross and the segregating F_3 lines gave good fits to a single gene hypothesis ratios. A single dominant gene hypothesis was supported highly by the genetic analysis of F_2, backcross and F_3 populations tested with the Mex-EB-83 isolate.

Using the Mor-BM-77 isolate, the F_2 population from PI. 382471 × Betzes gave results suggesting a single recessive gene segregation. The backcross and F_3 populations further confirmed this hypothesis. Similarly a single recessive gene was detected using Eth-HT-83 isolate.

It is very likely that PI. 382471 had different genes conditioning resistance to the different isolates tested since the reaction of the 32 individual F_3 lines was not the same to any two isolates.

PI. 382488

PI. 382488 was resistant to all seven isolates investigated at 21 C.

The F_2 progeny from the cross of PI. 382488 with Betzes segregated in ratios not significantly different from the ratios expected if resistance in this cultivar was controlled by a single dominant gene to US-MT-83 and US-CA-83 isolates. The backcross and F_3 populations further supported this result. It seems that two different genes in PI. 382488 conditioned resistance to US-MT-83 and US-CA-83 isolates as the same F_3 lines gave different reaction to the two isolates.

When inoculated with Mor-BM-77 isolate, the segregation of F_2 progeny from the same cross indicated that resistance in PI. 382488 was controlled by a single recessive gene. This was further supported by results from backcross and F_3 tests. The results obtained with F_2 progeny from the same cross indicated that PI. 382488 contained a single recessive gene for resistance to the Eth-DZ-83 isolate.

PI. 382509

PI. 382509 was resistant to Eth-HT-83, US-CA-83, US-MT-83, Mex-EB-83 and Mor-BM-77 isolates (Table 1).

In a test with US-MT-83 isolate and F_2 plants from PI. 382509 × Betzes the segregation gave a satisfactory fit to a 9:7 ratio. The segregating F_3 lines gave a fit to a ratio of

either 3:1 or 9:7 even though a very poor fit to a ratio of 1 resistant:8 segregating:7 susceptible families was observed. This may be due to the non-randomness of the F_3 sample. These results indicated that two complementary dominant genes are involved in PI. 382509 conditioning resistance to the US-MT-83 isolate. Segregation to US-CA-83, Mex-EB-83 and Eth-HT-83 isolates in the same cross suggested monogenic resistance in PI. 382509 to these isolates. Since the individual F_3 lines did not react the same to any two or more isolates, it is probable that different genes conferred resistance to the different isolates. Analysis of F_2, backcross and F_3 populations tested with Mor-BM-77 isolate indicated that a single recessive gene in PI. 382509 conditioned resistance to this isolate.

PI. 383036

This cultivar was resistant to all of the isolates used in this investigation. It was impossible to use this cultivar as a female parent since it was cleistogamous.

Tests of F_2, backcross and F_3 populations from Betzes × PI. 383036 with US-MT-83, US-CA-83 and Eth-HT-83 isolates showed that the resistance of PI. 383036 was governed by a single dominant gene (Table 2). However, a single recessive gene was detected using Mex-EB-83, Mor-BM-77, Eth-DZ-83 and Tun-BJ-81 isolates. The reaction of the individual F_3 lines was different to the isolates again indicating that different genes were responsible for conditioning resistance to the different isolates.

Atlas, Turk, La Mesita, Trebi, Brier, CI. 3940 and Modoc

The inheritance of resistance to scald in these cultivars has been investigated by different workers.

A single dominant gene, designated Rh, in Brier, conditioned resistance to scald (Bryner, 1957; Dyck and Schaller, 1961; Habgood and Hayes, 1971; Starling et al., 1971). In tests with US-MT-83 on 488 F_2 plants from a Betzes × Brier cross the segregation gave an

excellent fit to a 3:1 ratio indicating that a single dominant gene gave resistance to US-MT-83 isolate. It was assumed that this gene was the one designated as Rh by other workers.

CI. 3940 is of Ethiopian origin. Harrabi (1982) first studied the genetics of resistance in this cultivar. He reported one recessive and one dominant gene for resistance to Morocco and Tunisian isolates respectively. In a cross of Betzes × CI. 3940, 196 F_2 plants when tested with US-MT-83 isolate segregated to fit a 3:1 ratio. This result indicated that CI. 3940 has a single dominant gene for resistance to the US-MT-83 isolate.

Atlas was reported to possess a single dominant gene, Rh2, for scald resistance (Dyck and Schaller, 1961a; Starling et al., 1971). In tests with US-MT-83 and Eth-HT-83 isolates, F_2 populations from an Atlas × Betzes cross segregated to give a good fit to a 3:1 ratio confirming the previous reports.

Dyck and Schaller (1961) designated two dominant genes, Rh3 and Rh5, for scald resistance in Turk, whereas, other workers (Baker and Larter, 1963; Evans, 1969; Starling et al., 1971; Wells and Skoropad, 1963) reported only a single dominant gene. In this investigation a single dominant gene for resistance was detected in Turk using the US-MT-83 isolate and F_2 population from a Turk × Betzes cross.

Dyck and Schaller (1961) reported a single dominant gene, Rh4, for scald resistance in both La Mesita and Trebi. Modoc had an allele at the Rh4 locus (Dyck and Schaller, 1961). The results obtained with F_2 progeny from crosses with Betzes indicated that La Mesita, Trebi and Modoc each contained a single dominant gene for resistance to the US-MT-83 isolate. Two complementary recessive genes were detected in Modoc with the Mor-BM-77 isolate. Riddle and Briggs (1950), using a mixture of six cultures of *R. secalis,* reported Modoc to possess a single dominant and a recessive gene for resistance.

Atlas 46 and Osiris

The results obtained with F_2 and F_3 progeny from an Atlas 46 × Betzes cross showed that Atlas 46 had two independent dominant genes for resistance to the US-MT-83 isolate. This confirmed the previous reports by Dyck and Schaller (1961) and Starling et al. (1971). Dyck and Schaller (1961) designated these two resistance genes in Atlas 46 as Rh2 and Rh3. It was assumed that the same two genes, Rh2 and Rh3, were identified in the present study.

Osiris was resistant to all of the isolates in this investigation. The F_2 progeny from a cross between Osiris and Betzes segregated to give a good fit of 15 resistant:1 susceptible plants in response to US-MT-83 isolate. Dyck and Schaller (1961) reported a single dominant gene, Rh4, for scald resistance in Osiris, whereas Habgood and Hayes (1971) found two complementary genes, Rh^4 and Rh10, in Osiris.

Jet and Nigrinudum

Previous workers concluded that resistance in Jet is governed by two complementary recessive genes (Baker and Larter, 1963; Habgood and Hayes, 1971). These genes were assigned symbols rh6 and rh7. The genetic analysis made on the basis of F_2 populations from a Betzes × Jet cross showed that Jet contained a single recessive gene and two recessive genes conditioning resistance to Eth-DZ-83 and US-MT-83 isolates, respectively. It is possible that only one of the two recessive genes conditioned resistance to the Eth-DZ-83 isolate.

A single recessive gene was detected in Nigrinudum when F_2 populations from a Nigrinudum × Betzes cross were tested with US-MT-83 and Eth-DZ-83 isolates. It was assumed that this gene was the one designated rh8 by Wells and Skoropad (1963). Habgood and Hayes (1971) also reported a single recessive gene for resistance in Nigrinudum.

Kitchin

The results from the cross Kitchin × Betzes indicated a single gene for resistance, since the F_2 population segregated in the ratio of 3 resistant:1 susceptible plants. Of the 69 F_2 plants in the resistant category (Table 2), 47 plants developed some scald symptoms on their second leaves. Classifying these as intermediates, the F_2 population exhibited a good fit to a ratio of 1 resistant:2 intermediate:1 susceptible plants suggesting that the gene in Kitchin was partially dominant. This was in agreement with the previous work of Baker and Larter (1963). These workers gave the symbol Rh9 to the gene for scald resistance in Kitchin.

Resistant × Resistant Crosses

An attempt was made to determine the relationship of the resistance genes in the Ethiopian barley cultivars when tested with US-MT-83 and Mor-BM-77 isolates with some previous reports using other isolates. The results from testing the F_2 generations of various crosses among resistant cultivars are presented in Tables 3, 4, 5, 6, and 7.

PI. 382282

The results from PI. 382282 crossed with other resistant cultivars are presented in Table 3. Susceptible segregates were obtained from crosses involving Atlas, Turk, Osiris, La Mesita, Trebi, Modoc, Nigrinudum, Kitchin, and PI. 383036 when tested with the US-MT-83 isolate. This indicated that the genes in PI. 382282 conditioning resistance to US-MT-83 are different from those in these cultivars. No susceptible plants were found from PI. 382282 × Atlas 46 cross. However, the F_2 population tested was not large enough to detect segregation for four genes. Moreover, Atlas 46 was derived from the backcrossing program for incorporating scald resistance from Turk (transfer of the Rh3 gene) into Atlas (Rh2) and in most studies it was demonstrated that Atlas 46 possessed Rh2 and Rh3 genes (Dyck

Table 3. The Reaction of F_2 Progeny From Crosses of PI. 382282 With Other Resistant Cultivars to Isolates of *Rhynchosporium secalis*.

Cross	Isolate	Res.	Susc.	Expected Ratio	Probability
PI. 382282 × CI. 3940	US-MT-83	212	–	57:7	.00
PI. 382282 × CI. 3940	Mor-BM-77	116	–	7:9	.00
PI. 382282 × Atlas	US-MT-83	168	15	57:7	.28
PI. 382282 × Atlas 46	US-MT-83	108	–	249:7	.20
PI. 382282 × Turk	US-MT-83	91	2	57:7	.01
PI. 382282 × Osiris	US-MT-83	97	10	249:7	.00
PI. 382282 × La Mesita	US-MT-83	91	6	57:7	.18
PI. 382282 × La Mesita	Mex-EB-83	126	12	57:7	.48
PI. 382282 × Trebi	US-MT-83	91	10	57:7	.86
PI. 382282 × Modoc	US-MT-83	81	9	57:7	.91
PI. 382282 × Jet	US-MT-83	180	10	193:63	.00
PI. 382282 × Nigrinudum	US-MT-83	83	19	43:21	.003
PI. 382282 × Kitchin	US-MT-83	103	21	57:7	.05
PI. 382282 × PI. 382488	US-MT-83	230	–	57:7	.00
PI. 382282 × PI. 382488	Mor-BM-77	202	–	7:9	.00
PI. 382282 × PI. 382509	US-MT-83	244	–	205:51	.00
PI. 382282 × PI. 382509	Mor-BM-77	229	–	7:9	.00
PI. 382282 × PI. 383036	US-MT-83	241	33	57:7	.62
PI. 382282 × PI. 383036	Mor-BM-77	174	47	7:9	.00
PI. 382471 × PI. 382282	US-MT-83	276	–	57:7	.00
PI. 382472 × PI. 382282	Mor-BM-77	116	–	7:9	.00

and Schaller, 1961). Since PI. 382282 segregated in the crosses with Atlas and Turk, the apparent absence of susceptible segregates in the cross with Atlas 46 could be attributed to the inadequate F_2 population size.

No susceptible plants were found in F_2 progeny from crosses involving CI. 3940, PI. 382471, PI. 382488 and PI. 382509 when tested with US-MT-83 isolate suggesting that one of the genes in PI. 382282 was either situated at the locus carrying the genes in these cultivars or closely linked. The results obtained with F_2 and F_3 progeny from crosses with Betzes showed that PI. 382282, CI. 3940, PI. 382488, PI. 382509, PI. 383036 and PI. 382471 each contained a single recessive gene for resistance to Mor-BM-77 isolate (Table 2). Crosses of PI. 382282 with these cultivars, with the exception of PI. 383036, produced F_2 populations which were completely resistant showing that the genes are at the same locus (Table 3). Susceptible plants were obtained in the cross with PI. 383036 indicating that the recessive genes in PI. 382282 and PI. 383036 are different. However, the occurrence of excess resistant plants could not be explained in this study. If this result was obtained due to very close linkage and no recombinant types were recovered, a ratio of 1:1 or close to it should have been attained.

PI. 382471

Table 4 shows the results obtained with F_2 progeny from crosses of PI. 382471 with other resistant cultivars.

The gene in PI. 382471 for resistance to US-MT-83 (Table 2) was different from those in Brier (Rh), Atlas (Rh2), Atlas 46 (Rh2 + Rh3), Turk (Rh3), Osiris (Rh4 + Rh10), La Mesita (Rh4), Trebi (Rh4), Modoc ($Rh4^2$), Jet (rh6 + rh7), Nigrinudum (rh8) and Kitchin (Rh9), as susceptible F_2 plants appeared in crosses involving these cultivars. It was assumed that the resistance genes to US-MT-83 detected in these previously studied cultivars were the same as those reported by other workers.

Table 4. The Reaction of F_2 Progeny From Crosses of PI. 382471 With Other Resistant Parents to Isolates of *Rhynchosporium secalis*.

Cross	Isolate	Observed Frequency		Expected Ratio	Probability
		Res.	Susc.		
PI. 382471 X Brier	US-MT-83	115	7	15:1	.96
PI. 382471 X CI. 3940	US-MT-83	102	–	15:1	.02
PI. 382471 X CI. 3940	Mor-BM-77	214	–	7:9	.00
PI. 382471 X Atlas	US-MT-83	131	10	15:1	.81
PI. 382471 X Atlas 46	US-MT-83	124	11	63:1	.00
PI. 382471 X Turk	US-MT-83	144	3	15:1	.05
PI. 382471 X Osiris	US-MT-83	141	4	63:1	.41
PI. 382471 X La Mesita	US-MT-83	134	6	15:1	.43
PI. 382471 X Trebi	US-MT-83	138	11	15:1	.69
PI. 382471 X Modoc	US-MT-83	132	14	15:1	.13
PI. 382471 X Jet	US-MT-83	116	9	55:9	.04
PI. 382471 X Nigrinudum	US-MT-83	120	2	13:3	.00
PI. 382471 X Kitchin	US-MT-83	150	2	15:1	.003
PI. 382471 X PI. 382488	US-MT-83	255	–	15:1	.00
PI. 382471 X PI. 382488	Mor-BM-77	171	–	7:9	.00
PI. 382471 X PI. 382509	US-MT-83	234	–	57:7	.00
PI. 382471 X PI. 382509	Mor-BM-77	211	–	7:9	.00
PI. 382471 X PI. 383036	US-MT-83	172	2	15:1	.01
PI. 382471 X PI. 383036	Mor-BM-77	155	20	7:9	.00

The PI. 382471 gene for the US-MT-83 isolate appeared to be allelic to the gene in CI. 3940, since no recombinant types were observed in 102 F_2 plants. If two tightly linked genes were involved, the size of this F_2 population limited to the maximum amount of 2.9 percent recombination. An intercross between these two cultivars gave an F_2 population which was completely resistant to Mor-BM-77 isolate, suggesting that the recessive genes for resistance to this isolate were at the same locus. No recombinants were obtained in the crosses involving PI. 382488, PI. 382509 and PI. 382282 to US-MT-83 isolate which suggested that PI. 382471 had either a gene in common with these cultivars or a closely linked genes. The completely resistant F_2 plants obtained from the crosses of PI. 382471 with PI. 382488 and PI. 382509 in the test with Mor-BM-77 isolate demonstrated that the recessive genes in these cultivars are at the same locus. Even though the appearance of recombinant types from the cross PI. 382471 × PI. 383036 to Mor-BM-77 isolate was an indication for the presence of different genes in the cultivars, no explanation was found for the extreme deficiency of susceptible plants.

PI. 382488

Table 5 presents results from crosses of PI. 382488 with other resistant cultivars. The absence of recombinants in the cross with CI. 3940 suggested that the genes in these cultivars are situated at the same locus through separate loci up to 2-8 cross-over units apart could give the same result. The recessive genes in these cultivars were at the same locus since no recombinant types were recovered in the test of 222 F_2 plants with Mor-BM-77 isolate. The same result was attained with regard to the PI. 382509 resistance gene to the Mor-BM-77 isolate.

The absence of susceptible plants in the cross with Atlas 46 was attributed to the insufficient number of F_2 plants to detect segregation for three genes rather than to allelism or close linkage. The resistance gene to US-MT-83 isolate in PI. 382488 was different from

Table 5. The Reaction of F_2 Progeny From Crosses of PI. 382488 and Other Resistant Cultivars to Isolates of *Rhynchosporium secalis*.

Cross	Isolate	Observed Frequency		Expected Ratio	Probability
		Res.	Susc.		
PI. 382488 × CI. 3940	US-MT-83	111	–	15:1	.01
PI. 382488 × CI. 3940	Mor-BM-77	222	–	7:9	.00
PI. 382488 × Atlas	US-MT-83	126	10	15:1	.72
PI. 382488 × Atlas 46	US-MT-83	113	–	63:1	.34
PI. 382488 × Turk	US-MT-83	92	5	15:1	.81
PI. 382488 × Osiris	US-MT-83	206	9	63:1	.004
PI. 382488 × La Mesita	US-MT-83	222	9	15:1	.18
PI. 382488 × Trebi	US-MT-83	195	16	15:1	.51
PI. 382488 × Modoc	US-MT-83	264	12	15:1	.24
PI. 382488 × Jet	US-MT-83	244	25	55:9	.03
PI. 382488 × Nigrinudum	US-MT-83	206	18	13:3	.00
PI. 382488 × Kitchin	US-MT-83	258	24	15:1	.15
PI. 382488 × PI. 382509	US-MT-83	141	–	57:7	.001
PI. 382488 × PI. 382509	Mor-BM-77	193	–	7:9	.00
PI. 382488 × PI. 383036	US-MT-83	103	7	15:1	.88
PI. 382488 × PI. 383036	Mor-BM-77	114	41	7:9	.00

those in Atlas, Turk, Osiris, La Mesita, Trebi, Modoc, Jet, Nigrinudum, Kitchin and PI. 383036 as indicated by segregation.

PI. 382509

The segregation of the progeny from crosses of PI. 382509 with the other resistant cultivars in the test with US-MT-83 and Mor-BM-77 isolates are shown in Table 6. Crosses with all but CI. 3940 and Kitchin gave recombinant types. Susceptible plants were, however, obtained in the cross with Kitchin in the field. The cross between PI. 382509 and CI. 3940 produced resistant F_2 plants when tested with Mor-BM-77 isolate showing that the genes for resistance to this isolate had the same locus. A close linkage was noticed between the genes in PI. 382509 and PI. 383036 conferring resistance to Mor-BM-77 isolate as the F_2 progeny from the cross involving these two cultivars gave a poor fit to a 7:9 ratio. The poor fit to the expected ratio in the cross with Osiris was due to an excess of susceptible plants that could happen by chance alone.

PI. 383036

The results from crosses between PI. 383036 and various resistant cultivars are presented in Table 7. It was interesting to see the segregation pattern in these crosses. No susceptible segregates in crosses with cultivars possessing Rh, Rh3 and Rh4 resistance genes were observed. These results suggested that the gene in PI. 383036 was allelic or tightly linked with the Rh-Rh3-Rh4 locus. The absence of any susceptible segregates from the cross of Jet with PI. 383036 suggested that one of the recessive genes in Jet was allelic or closely linked to the dominant gene detected in PI. 383036. Starling et al. (1971) emphasized the predominance of the Rh-Rh3-Rh4 locus for resistance to *R. secalis* in the cultivars they studied. Of the 5 new Ethiopian barleys studied, PI. 383036 was the only one showing allelism or close linkage with this locus.

Table 6. The Reaction of F_2 Progeny From Crosses of PI. 382509 With Other Resistant Cultivars to Isolates of *Rhynchosporium secalis.*

Cross	Isolate	Observed Frequency		Expected Ratio	Probability
		Res.	Susc.		
PI. 382509 X Brier	US-MT-83	227	16	57:7	.03
PI. 382509 X CI. 3940	US-MT-83	164	–	57:7	.00
PI. 382509 X CI. 3940	Mor-BM-77	242	–	7:9	.00
PI. 382509 X Atlas	US-MT-83	275	20	57:7	.03
PI. 382509 X Atlas 46	US-MT-83	278	12	249:7	.20
PI. 382509 X Turk	US-MT-83	217	17	57:7	.10
PI. 382509 X Osiris	US-MT-83	203	15	249:7	.00
PI. 382509 X La Mesita	US-MT-83	252	20	57:7	.10
PI. 382509 X Trebi	US-MT-83	271	15	57:7	.003
PI. 382509 X Modoc	US-MT-83	266	14	57:7	.01
PI. 382509 X Jet	US-MT-83	198	30	193:63	.00
PI. 382509 X Nigrinudum	US-MT-83	249	36	43:21	.00
PI. 382509 X Kitchin	US-MT-83	259	–	57:7	.00
PI. 382509 X PI. 383036	US-MT-83	226	15	57:7	.03
PI. 382509 X PI. 383036	Mor-BM-77	129	102	7:9	.00

Table 7. The Reaction of F_2 Progeny From Crosses of PI. 383036 With Other Resistant Parents to Isolates of *Rhynchosporium secalis*.

Cross	Isolate	Observed Frequency		Expected Ratio	Probability
		Res.	Susc.		
Brier X PI. 383036	US-MT-83	244	–	15:1	.00
CI. 3940 X PI. 383036	US-MT-83	337	13	15:1	.1
CI. 3940 X PI. 383036	Mor-BM-77	226	26	7:9	.00
Atlas X PI. 383036	US-MT-83	243	29	15:1	.004
Atlas 46 X PI. 383036	US-MT-83	212	–	63:1	.12
Turk X PI. 383036	US-MT-83	210	–	15:1	.00
Osiris X PI. 383036	US-MT-83	255	–	63:1	.10
La Mesita X PI. 383036	US-MT-83	229	–	15:1	.00
Modoc X PI. 383036	US-MT-83	217	–	15:1	.00
Jet X PI. 383036	US-MT-83	225	–	55:9	.00
Nigrinudum X PI. 383036	US-MT-93	195	35	13:3	.20

Field Reaction of Adult F_2 Plants

Acceptable fits to expected ratios based on a single dominant gene were obtained in segregating populations from the crosses involving Betzes with PI. 382471, PI. 382488 and PI. 383036 under field conditions. The F_2 populations from the crosses involving PI. 382282 and PI. 382509 gave good fits to 9:7 ratios (Table 8). These results are in agreement with those obtained under controlled environment (Table 2).

Table 8. The Reaction of Adult F_2 Progeny From Crosses Involving Betzes to US-MT-83 Isolate of *Rhynchosporium secalis* in the Field.

Cross	Res.	Susc.	Ratio	Probability
PI. 382282 X Betzes	89	55	9:7	.21
PI. 382471 X Betzes	91	35	3:1	.54
PI. 382488 X Betzes	117	47	3:1	.32
PI. 382509 X Betzes	55	37	9:7	.56
Betzes X PI. 383036	67	25	3:1	.72

In crosses of the resistant cultivars PI. 382282 and PI. 392509 with La Mesita, Trebi, Modoc, Jet and Nigrinudum, which are all susceptible to US-MT-83 isolate in the field, however, different segregation patterns were obtained that gave closer fits to ratios for a single gene hypothesis than any other hypothesis except the F_2 from the crosses involving La Mesita and Trebi (Tables 9, 12).

The results shown in Table 8 were obtained after third classification date. More susceptible plants were found in the last classification.

The F_2 progeny from crosses of Trebi, Modoc, Jet, and Nigrinudum with PI. 382471 all segregated in ratios not significantly different from the ratios expected if resistance in PI. 382471 was controlled by a single dominant gene. However, the F_2 from the cross PI. 382471 X La Mesita produced an excess of resistant plants (Table 10).

The results obtained with F_2 progeny from crosses of PI. 382488 with Trebi and Modoc indicated that PI. 382488 had a single dominant gene for resistance to US-MT-83

Table 9. The Reaction of Adult F_2 Progeny From Crosses Involving PI. 382282 to US-MT-83 Isolate of *Rhynchosporium secalis* in the Field.

Cross	Res.	Susc.	Ratio	Probability
PI. 382282 × CI. 3940	106	–	57:7	.00
PI. 382282 × Atlas	114	5	57:7	.03
PI. 382282 × Atlas 46	104	1	249:7	.41
PI. 382282 × Turk	104	5	57:7	.10
PI. 382282 × Osiris	116	–	249:7	.13
PI. 382282 × La Mesita (s)	99	6	(15:1)*	.98
PI. 382282 × Trebi (s)	71	19	(3:1)	.47
PI. 382282 × Modoc (s)	85	35	(3:1)	.34
PI. 382282 × Jet (s)	80	29	(3:1)	.78
PI. 382282 × Nigrinudum (s)	82	24	(3:1)	.65
PI. 382282 × Kitchin	115	10	57:7	.36
PI. 382282 × PI. 382488	156	–	57:7	.00
PI. 382282 × PI. 382509	164	–	205:51	.00
PI. 382282 × PI. 383036	155	–	57:7	.00
PI. 382471 × PI. 383036	128	–	57:7	.00

*Ratios in parenthesis are not expected but give best fit.

Table 10. The Reaction of Adult F_2 Progeny From Crosses Involving PI. 382471 to US-MT-83 Isolate of *Rhynchosporium secalis* in the Field.

Cross	Res.	Susc.	Ratio	Probability
PI. 382471 × Brier	138	6	15:1	.42
PI. 382471 × CI. 3940	123	–	15:1	.00
PI. 382471 × Atlas	138	8	15:1	.83
PI. 382471 × Atlas 46	116	–	63:1	.32
PI. 382471 × Turk	133	4	15:1	.15
PI. 382471 × Osiris	132	–	63:1	.27
PI. 382471 × La Mesita (s)	121	15	3:1	.00
PI. 382471 × Trebi (s)	116	31	3:1	.33
PI. 382471 × Modoc (s)	115	30	3:1	.27
PI. 382471 × Jet (s)	102	33	3:1	.99
PI. 382471 × Nigrinudum (s)	95	22	3:1	.15
PI. 382471 × Kitchin	112	18	15:1	.00
PI. 382471 × PI. 382488	156	–	15:1	.00
PI. 382471 × PI. 382509	118	–	57:7	.00
PI. 382471 × PI. 383036	147	–	15:1	.00

isolate in the field. The F_2 populations from the crosses involving La Mesita and Nigrinudum gave poor fits to 3:1 ratios giving a deficiency of susceptible plants (Table 11). There was an excess of susceptible plants in the cross PI. 382488 × Jet.

Table 11. The Reaction of Adult F_2 Progeny From Crosses Involving PI. 382488 to US-MT-83 Isolate of *Rhynchosporium secalis* in the Field.

Cross	Res.	Susc.	Ratio	Probability
PI. 382488 × CI. 3940	107	–	15:1	.01
PI. 382488 × Atlas	137	6	15:1	.40
PI. 382488 × Atlas 46	101	–	63:1	.39
PI. 382488 × Turk	139	10	15:1	.95
PI. 382488 × Osiris	124	3	63:1	.71
PI. 382488 × La Mesita (s)	109	11	3:1	.00
PI. 382488 × Trebi (s)	80	34	3:1	.28
PI. 382488 × Modoc (s)	97	34	3:1	.88
PI. 382488 × Jet (s)	49	83	3:1	.00
PI. 382488 × Nigrinudum (s)	109	19	3:1	.01
PI. 382488 × Kitchin	105	14	15:1	.02
PI. 382488 × PI. 382509	117	–	57:7	.00
PI. 382488 × PI. 383036	127	–	15:1	.01

Table 12. The Reaction of Adult F_2 Progeny From Crosses Including PI. 382509 to US-MT-83 Isolate of *Rhynchosporium secalis* in the Field.

Cross	Res.	Susc.	Ratio	Probability
PI. 382509 × Brier	113	11	57:7	.55
PI. 382509 × CI. 3940	132	–	57:7	.00
PI. 382509 × Atlas	130	19	57:7	.56
PI. 382509 × Atlas 46	158	3	249:7	.66
PI. 382509 × Turk	107	12	57:7	.88
PI. 382509 × Osiris	116	–	249:7	.13
PI. 382509 × La Mesita (s)	112	23	(3:1)*	.04
PI. 382509 × Trebi (s)	120	9	(15:1)	.87
PI. 382509 × Modoc (s)	119	39	(3:1)	1.0
PI. 382509 × Jet (s)	97	24	(3:1)	.23
PI. 382509 × Nigrinudum (s)	115	38	(3:1)	.96
PI. 382509 × Kitchin	127	10	57:7	.23
PI. 382509 × PI. 383036	146	1	57:7	.00

*Ratios in parenthesis are not expected but give best fit.

The segregation of the progeny from crosses involving PI. 383036 with La Mesita, Trebi, Modoc, Jet and Nigrinudum are shown in Table 13. The segregations were incompatible with the hypothesis that resistance in PI. 383036 was conferred by a single dominant gene. Field classifications could be uncertain particularly if disease readings were taken only once.

Table 13. The Reaction of Adult F_2 Progeny From Crosses Involving PI. 383036 to US-MT-83 Isolate of *Rhynchosporium secalis* in the Field.

Cross	Res.	Susc.	Ratio	Probability
Brier × PI. 383036	117	2	15:1	.06
CI. 3940 × PI. 383036	140	–	15:1	.00
Atlas × PI. 383036	157	4	15:1	.07
Atlas 46 × PI. 383036	140	–	63:1	.25
Turk × PI. 383036	141	–	15:1	.00
Osiris × PI. 383036	141	–	63:1	.25
La Mesita × PI. 383036	144	2	(63:1)*	.88
Trebi × PI. 383036	134	10	(15:1)	.86
Modoc × PI. 383036	133	25	(13:3)	.40
Jet × PI. 383036	133	2	(63:1)	.79
Nigrinudum × PI. 383036	145	2	(63:1)	.89

*Ratios in parenthesis are not expected but give best fit.

Segregation Patterns in Susceptible × Susceptible Crosses

F_2 and F_3 seedling progeny of crosses between Betzes and some Ethiopian barley cultivars were tested with isolates to which the latter were susceptible. The results are presented in Table 14.

Habgood and Hayes (1974) reported transgressive segregation for scald resistance in some European spring barley cultivars. Transgression towards resistance has been reported for a number of other diseases (Krupinsky and Sharp, 1978; Scharen and Bryan, 1979; Sharp and Volin, 1970).

Transgressive segregation for scald resistance was observed in most cross combinations in the F_2 and F_3 materials. The resistant F_2 plants observed were reinoculated to make

Table 14. The Reaction of Seedling Progeny of Crosses Between Susceptible × Susceptible Cultivars to Isolates of *Rhynchosporium secalis.*

Cross	Generation	Isolate	Res.	Segr.	Susc.
PI. 382282* × Betzes	F_2	Eth-HT-83	7	—	88
PI. 382282 × Betzes	F_2	Eth-DZ-83	5	—	185
PI. 382282 × Betzes	F_3	Eth-DZ-83	—	1	31
PI. 382282 × Betzes	F_2	Tun-BJ-81	—	—	177
PI. 382282 × Betzes	F_3	Tun-BJ-81	—	15	17
PI. 382471 × Betzes	F_2	Eth-DZ-83	5	—	229
PI. 382471 × Betzes	F_3	Eth-DZ-83	—	22	10
PI. 382471 × Betzes	F_2	Tun-BJ-81	6	—	208
PI. 382471 × Betzes	F_3	Tun-BJ-81		2	30
PI. 382488† × Betzes	F_2	Eth-HT-83	34	—	100
PI. 382488† × Betzes	F_2	Tun-BJ-81	15	—	130
PI. 382488† × Betzes	F_2	Mex-EB-83	27	—	102
PI. 382509 × Betzes	F_2	Eth-DZ-83	2	—	168
PI. 382509 × Betzes	F_3	Eth-DZ-83	—	18	14
Trebi × Betzes	F_2	Mor-BM-77	4	—	44

*PI. 382282 is susceptible to Eth-HT-83 isolate at temperatures higher than 26 C.
†PI. 382488 is susceptible to the respective isolates at temperatures higher than 26 C.

sure that they were not escapes. PI. 382282 and PI. 382488 were as susceptible as Betzes at higher temperatures in the greenhouse. When the F_2 plants from the crosses with Betzes were kept at higher temperatures after inoculation, immune plants were recovered. A similar report has been given on some other barley cultivars by Harrabi (1982). Segregating lines occurred in all F_3 materials tested.

Reciprocal Crosses

Some reciprocal crosses were made to see if there was any difference between them. The response of F_2 plants to US-MT-83 isolate in the progeny of reciprocal crosses is presented in Table 15. Striking differences in interpretation of gene actions were observed in reciprocal crosses involving PI. 382282 and PI. 382471. The genetic interpretation remained the same in reciprocal crosses involving PI. 382509. In the Betzes × PI. 382282 cross more susceptible F_2 plants were obtained than in the cross made in the opposite direction. A similar situation occurred in crosses involving PI. 382471.

Table 15. The Reaction of F_2 Plants to US-MT-83 Isolate of *R. secalis* in the Progeny of Reciprocal Crosses.

Cross	Res.	Susc.	Ratio	Probability
Betzes X PI. 382282	26	120	3:13	.85
PI. 382282 X Betzes	126	105	9:7	.65
Betzes X PI. 382471	102	139	7:9	.70
PI. 382471 X Betzes	106	46	3:1	.16
Betzes X PI. 382509	132	100	9:7	.89
PI. 382509 X Betzes	103	88	9:7	.57

Incubation Period and Genetic Interpretation

Habgood and Hayes (1971) discovered that a single gene segregation apparent at a 14-day incubation period could be interpreted as the action of two complementary genes if re-examined at the end of a 28-day incubation period. F_2 materials from some crosses involving Betzes were classified at two different incubation periods, 10 and 14 days (Table 16). Scald symptoms developed sufficiently on Betzes and F_1 plants in 10 days. The F_2 progeny from all crosses shown in Table 16 segregated to give the interpretation of a dominant gene action when assessed 10 days after inoculation. When re-assessed 14 days after inoculation, a number of "resistant" plants showed very good scald symptoms indicating that recessive gene(s) were actually conditioning resistance in those Ethiopian cultivars to the particular isolates used.

Table 16. The Reaction of F_2 and F_1 Plants to Mor-BM-77* and US-MT-83† Isolates of *R. secalis* at Two Incubation Periods.

Cross/Cultivar	Generation	Days After Inoculation	Res.	Susc.	Ratio	Probability
PI. 382488 X Betzes	F_1	10	–	2		
PI. 382488 X Betzes	F_2	10	88	56	9:7	.33
PI. 382488	parent	10	5	–		
Betzes	parent	10	–	5		
PI. 382488 X Betzes	F_1	14	–	2		
PI. 382488 X Betzes	F_2	14	43	101	1:3	.21
PI. 381388	parent	14	5	–		
Betzes	parent	14	–	5		
PI. 382509 X Betzes	F_1	10	–	3		
PI. 382509 X Betzes	F_2	10	101	38	3:1	.59
PI. 382509	parent	10	5	–		
Betzes	parent	10	–	5		
PI. 382509 X Betzes	F_1	14	–	3		
PI. 382509 X Betzes	F_2	14	43	96	1:3	.13
Betzes X PI. 383036	F_1	10	–	3		
Betzes X PI. 383036	F_2	10	121	54	3:1	.01
PI. 383036	parent	10	6	–		
Betzes	parent	10	–	5		
Betzes X PI. 383036	F_1	14	–	3		
Betzes X PI. 383036	F_2	14	45	130	1:3	.90
PI. 382471 X Betzes	F_1	10	–	5		
PI. 382471 X Betzes	F_2	10	78	60	9:7	.97
PI. 382471	parent	10	6	–		
Betzes	parent	10	–	5		
PI. 382471 X Betzes	F_1	14	–	5		
PI. 382471 X Betzes	F_2	14	38	100	1:3	.56
Betzes X Jet	F_2	10	144	55	3:1	.44
Betzes	parent	10	–	6		
Jet	parent	10	5	–		
Betzes X Jet	F_2	14	80	119	7:9	.35

*Crosses involving PI. 382488, PI. 382509, PI. 383036, and PI. 382471 were tested against Mor-BM-77 isolate.

†The cross Betzes X Jet was tested against US-MT-83 isolate.

CHAPTER 5

DISCUSSION

Genetic information on available sources of resistant germ plasm is useful for the development of scald resistant varieties.

Resistance genes which may not be effective for control against pathogen populations in one location need not necessarily be ineffective in another. Jackson and Webster (1976) found Atlas 46 to be susceptible to more than 250 isolates from California, whereas, it was resistant to 35 distinct races of *R. secalis* from South Australia as reported by Ali et al. (1976). No two isolates used in this study induced the same reactions on all 18 cultivars tested. All cultivars except Trebi gave the same reactions to both Mex-EB-83 and Mor-BM-77 isolates. It was interesting to note that using Mor-BM-77 isolate only recessive resistance genes were detected in different cultivars (Table 2). According to gene-for-gene relationships, resistance can be conferred on the host by any resistance allele that is not matched by a related virulence allele. If gene-for-gene relationships operate in this parasitic system, avirulence in Mor-BM-77 isolate is probably dominant. The more virulent of the two Ethiopian isolates, Eth-DZ-83, was collected from Debre Zeit area where barley scald and barley are of little importance. Its virulence probably helped the fungus in attacking the very few available barley cultivars in the area.

Ali et al. (1976) reported that the genes for resistance in Atlas 46 have complementary effects. They observed that pathotypes pathogenic on both Atlas and Turk were not pathogenic on Atlas 46, a derivative of a cross between Atlas and Turk and which in several

studies has been found to contain the genetic components for scald resistance of both parents. This complementary gene effect has not been observed in this study. Atlas, Turk and Atlas 46 were susceptible to US-CA-83 and Tun-BJ-81 isolates.

The resistance in PI. 382282 and PI. 382488 was impaired by temperatures above 26 C to certain isolates (Table 1). The value of these cultivars as parental stocks in a breeding program is reduced due to their temperature sensitive reaction. It was observed that temperatures that caused a "breakdown" of resistance in PI. 382282 and PI. 382488 did not affect resistance in PI. 382471, PI. 382509 and PI. 383036. Baker and Larter (1963) noted that temperatures above 25 C during the infection period caused a breakdown of resistance in the varieties Jet and Steudelli (CI. 2226). The temperature sensitive reaction of Jet was confirmed in the course of the present investigation. It was interesting to note that all of these cultivars with temperature sensitive resistance genes, PI. 382282, PI. 382488, Jet and Steudelli, are of Ethiopian origin.

PI. 382282 and PI. 382509 show identical patterns in inheritance of resistance and reaction to the seven test isolates. This suggests that the resistance genes, at least to US-MT-83 and Mor-BM-77 isolates, are identical. Each of these cultivars contained a single dominant gene for resistance to US-CA-83 isolate. One of the two complementary dominant genes conferring resistance to US-MT-83 isolate was probably responsible for resistance to US-CA-83 isolate. PI. 382509 possessed a single dominant gene conditioning resistance to Mex-EB-83 isolate. Again one of the two complementary genes detected using US-MT-83 isolate might singly condition the resistance to Mex-EB-83 isolate. It was, however, important to emphasize that the dominant gene in PI. 382509 conditioning resistance to US-CA-83 isolate was different from the one responsible for Mex-EB-83 resistance since the individual F_3 lines from the cross PI. 382509 × Betzes reacted differently to the two isolates. A single recessive gene in PI. 382282 conditioned resistance to Mex-EB-83 isolate which was different from the one detected with Mor-BM-77 isolate.

The two complementary dominant genes in PI. 382282 and PI. 392509 were shown to be different from those previously reported and the symbols Rh12 and Rh13 are suggested for them.

The results obtained from crosses involving PI. 382471, PI. 382282, PI. 392488, PI. 382509 and CI. 3940 indicated that the resistance genes for Mor-BM-77 isolate in these cultivars were all located at the same locus. The recessive gene in PI. 383036 conferring resistance to Mor-BM-77 was found to be different from those in these cultivars. F_2 progeny from crosses of PI. 383036 with PI. 382282, PI. 382471, PI. 382488 and CI. 3940 produced extreme deficiency of susceptible plants which probably was due to some other factors besides tight linkage. Harrabi (1982) related the recessive gene in CI. 3940 to those in Steudelli, rh6 and rh7, using Mor. 25 (now Mor-BM-77) isolate. He found the gene in CI. 3940 to be allelic to one of those in Steudelli. Since the gene in CI. 3940 shared the same locus with those in PI. 382282, PI. 382471, PI. 382488 and PI. 382509, it was logical to assume that the recessive genes in these cultivars were allelic to one of the genes in Steudelli. The fact that if two genes show with one another a low cross-over value, they show nearly the same value, low or high, with any other gene, further supports this assumption. Both CI. 3940 and Steudelli are also of Ethiopian origin.

The symbol rh14 is suggested for the recessive gene in PI. 382282 conferring resistance to Mex-EB-83 isolate. Since the recessive gene in PI. 383036 for resistance to Mor-BM-77 was shown to be different from the others, the symbol rh15 is suggested for it.

The dominant gene in PI. 382471 for resistance to US-MT-83 isolate was either identical, allelic or closely linked to that in PI. 382488. These same genes in PI. 382471 and PI. 382488 were shown to be either identical, allelic or closely linked to one of the genes in PI. 382282 and PI. 382509. It was possible that the genes were identical but the difference that another complementary gene was required in PI. 382282 and PI. 382509 to confer full resistance could be due to differences in the genetic background in which the genes

were located. PI. 382471 and PI. 382488 each possessed a single dominant gene for resistance to US-CA-83 isolate which was different from the one for US-MT-83 isolate resistance. The relationship of these two genes in these cultivars was not determined using US-CA-83 isolate. Even though PI. 382471 and PI. 382488 gave different reactions to Eth-DZ-83 and Tun-BJ-81 isolates, they showed a similar pattern for inheritance of resistance. The symbol Rh16 is proposed for the dominant gene in PI. 382471 and possibly PI. 382488 conferring resistance to US-CA-83.

PI. 383036 appeared to be different from the other Ethiopian barley cultivars, and similar to some of the previously studied cultivars in terms of inheritance of resistance. No recombinants were observed in crosses of this cultivar with those possessing Rh, Rh3, and Rh4 resistance genes which indicated that the gene in PI. 383036 was allelic or tightly linked with the Rh-Rh3-Rh4 locus. Of the five new cultivars studied, PI. 383036 was the only one showing allelism or tight linkage to this locus.

Of the cultivars previously studied, Atlas (Rh2), Turk (Rh3), La Mesita (Rh4), Trebi (Rh4), Modoc ($Rh4^2$), Brier (Rh), CI. 3940, Kitchin (Rh9), and Nigrinudum (rh8) segregated on the basis of a single gene for resistance, and Atlas 46 (Rh2 + Rh3), Osiris (Rh4 + Rh10), and Jet (rh6 + rh7) on the basis of two genes. Since these results, both in terms of gene actions and number of genes, are in agreement with those of previous studies, it was assumed that the same previously reported genes were conditioning resistance to US-MT-83 isolate.

La Mesita, Trebi, Modoc, Jet and Nigrinudum were all susceptible to US-MT-83 isolate in the field. In crosses of the resistant cultivars with these, different segregation patterns were observed depending on the susceptible parent involved (Tables 9, 10, 11, 12, 13). As there is variation in the field, some susceptible F_2 plants could escape infection and thus be classified as resistant. It was also possible that some of the susceptible F_2 plants developed scald symptoms slower than others depending on the parents involved

resulting in no symptom expression at the time of classification. There were apparent differences in incubation periods among various scald susceptible cultivars in the field. Some cultivars showed scald symptoms in fewer days than others.

Transgressive segregation for scald resistance occurred in all cross combinations involving some European barley cultivars in F_3 material.

Significant differences in terms of disease expression were observed in reciprocal crosses involving Betzes with the cultivars PI. 382282 and PI. 382471, whereas the results from the reciprocal cross involving Betzes and PI. 382509 gave the same genetic interpretation (Table 15). The existence of extrachromosomal inheritance has been reported in other host-pathogen interactions (Dunn, 1974; Harland and King, 1957; Hooker, 1974; Nagaich et al., 1968; Prasad et al., 1975; Rath and Padmanabhan, 1972). Of all reciprocal crosses made, Harrabi (1982) reported a significant difference in one cross in his study of resistance to *R. secalis*. Even though significant differences were observed in some of the reciprocal crosses, this is suggestive but is not a solid proof for cytoplasmic inheritance. More work should be done to make a highly positive conclusion on the existence of cytoplasmic effect on scald reaction. For instance, one could substitute the genomes of PI. 382282 and PI. 382471 into the cytoplasm of Betzes by backcrossing and study scald reactions. It could be that the cytoplasmic factor of Betzes has more control over susceptibility to scald than do nuclear genes. In other cases, the interaction between nuclear genes and cytoplasmic genes could be so high that the nuclear genes predominate. In either case, PI. 382282 and PI. 382509 should have given similar results in reciprocal crosses with Betzes unless they differed in some modifier genes, since the resistance genes to US-MT-83 isolate in these cultivars were shown to be identical.

Differences in genetic interpretations could appear due to differences in incubation periods. Habgood and Hayes (1971) found genetic interpretation differences between classification made after a 14-day incubation and that after 28 days. Significant differences

were observed between classifications made after a 10-day and a 14-day incubation periods in this study (Table 16). It was assumed that this was a useful piece of information since some workers classified their segregating materials depending on when symptoms appeared on the susceptible cultivar they used. It is possible to be misled in such cases. The following was quoted from a paper by Starling et al. (1971).

> A pot of susceptible Wong was included in each flat to measure uniformity of inoculation and to determine the optimum date for evaluating the populations . . . Plants were classified for reaction to *R. secalis* depending on when symptoms on susceptible Wong were optimum for observation.

Harrabi (1982) reported that resistance in CI. 4354 to Mor. 25 isolate (designated as Mor-BM-77 in this study) was dominant based on the analysis of segregating F_2 material in the cross Betzes × CI. 4354, whereas all F_1 plants were susceptible. He gave no explanations as to how these contradicting results were obtained. Not all susceptible F_2 plants developed scald symptoms at the same time. Probably Harrabi (1982) did classification on F_2 plants before all susceptible plants developed symptoms. The incubation period after which first scald symptoms appeared on a susceptible check should not be taken as an appropriate period for classification of segregating materials. Reliable results were obtained if symptoms were evaluated at least 4 days after their first appearance.

CHAPTER 6

SUMMARY

1. New designations were given for scald isolates which included the country, particular place, and year of collection.
2. The genetics of scald resistance in 17 barley cultivars was investigated. Five resistance genes, shown to be different from previously known genes, were identified. The symbols Rh12 and Rh13 were proposed for the two complementary dominant genes in PI. 382282 and PI. 382509 for resistance to US-MT-83 isolate. The symbol rh14 was suggested for the recessive gene in PI. 382282 conferring resistance to Mex-EB-83 isolate. The symbol rh15 was proposed for the recessive gene in PI. 383036 conditioning resistance to Mor-BM-77 isolate. Rh16 was the designation suggested for the dominant gene in PI. 382471 and possibly PI. 382488 giving resistance to US-CA-83 isolate (Appendix, Table 20).
3. PI. 383036 was shown to possess a gene at the Rh-Rh3-Rh4 complex locus.
4. Transgressive segregation for scald resistance was observed in most cross combinations involving susceptible cultivars in F_2 and F_3 materials.
5. Indication was obtained for the existence of cytoplasmic effect on scald resistance in certain cross combinations.
6. An optimum incubation period was shown to be important for successful classification of segregating materials.
7. Only recessive genes in the different cultivars studied conditioned resistance to Mor-BM-77 isolate.

8. Care should be taken in using PI. 382282 and PI. 382488 as sources of scald resistance in a breeding program since they were shown to contain temperature sensitive resistance genes to certain isolates.

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APPENDIX

APPENDIX TABLES

Table 17. Barley Cultivars and Their Reactions to US-MT-83 Isolate of *R. secalis* Under Field Conditions in 1984.

Cultivar	Disease Reaction
PI. 382282	R
PI. 382471	R
PI. 382488	R
PI. 382509	R
PI. 383036	R
Betzes	S
Brier	R
Abyssinian	R
Atlas	R
Atlas 46	R
Turk	R
Osiris	R
La Mesita	S
Trebi	S
Modoc	S
Jet	S
Nigrinudum	S
Kitchin	R

Table 18. Resistance Genes to *Rhynchosporium secalis* in Barley.

Gene Symbol Assigned by Author	Cultivar in Which First Identified	Author(s)
Rh3	Turk (CI. 5611-2)	Dyck & Schaller (1961)
Rh4	La Mesita (CI. 7565)	Dyck & Schaller (1961)
$Rh^2 4$, Rh^2	Modoc (CI. 7566)	Dyck & Schaller (1961), Habgood & Hayes (1971)
Rha, Rh	Brier (CI. 7157)	Bryner (1957)
—	Trebi (CI. 936)	Riddle & Briggs (1950)
Rh2	Atlas (CI. 4118)	Dyck & Schaller (1961)
Rh5	Turk (CI. 5611-2)	Dyck & Schaller (1961)
rh8	Nigrinudum (CI. 2222)	Wells & Skoropad (1963)
rh6	Jet (CI. 967)	Baker & Larter (1963)
rh7, rh^5	Jet (CI. 967)	Baker & Larter (1963), Habgood & Hayes (1971)
Rh9	Kitchin (CI. 1296)	Baker & Larter (1963)
Rh^3	Wisconsin Winter × Glabron (CI. 8162)	Habgood & Hayes (1971)
Rh^4	Osiris (CI. 1622)	Habgood & Hayes (1971)
Rh10	Osiris (CI. 1622)	Habgood & Hayes (1971)
rh11	CI. 4364	Habgood & Hayes (1971)
—	CI. 3515	Starling et al. (1971)
—	CI. 8618	Starling et al. (1971)

Table 19. Barley Cultivars With Their Origin and Some Agronomic Characters.

Cultivar	Origin	Characters
PI. 382282	Ethiopia	Late, 2-rowed, white-seed
PI. 382471	Ethiopia	Late, 2-rowed, white seed
PI. 382488	Ethiopia	Late, 2-rowed, black seed
PI. 382509	Ethiopia	Relatively early, 2-rowed, black seed
PI. 383036	Ethiopia	Late, irregular head type, black seed
Betzes		2-rowed, white seed
Brier		Winter barley, 6-rowed, white seed
CI. 3940	Ethiopia	6-row, white seed
Atlas		6-row, white seed
Atlas 46		6-row, white seed
Turk	Turkey	2-row, white seed
Osiris		6-row, white seed
La Mesita	Egypt	6-row, white seed
Trebi	South Shore of Black Sea	6-row, white seed
Modoc		6-row, white seed
Jet	Ethiopia	2-row, hull-less, black seed
Nigrinudum	Ethiopia	2-row, hull-less, black seed
Kitchin		2-row, white seed

Table 20. Summary of Proposed Genes for Scald Resistance in Each Cultivar.

Gene	Cultivar	Remark
Rh12, Rh13	PI. 382282 PI. 382509	Independent of genes in Atlas, Atlas 46, Turk, Osiris, La Mesita, Trebi, Modoc, Jet, Nigrinudum, Kitchin
rh14	PI. 382282	Independent of genes in Jet
rh15	PI. 383036	Different from the recessive genes in PI. 382282, PI. 382471, PI. 382509, and CI. 3940
Rh16	PI. 382471	Independent of genes in PI. 382282, PI. 382509